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RAISING RABBITS IN A MOVING VISUAL ENVIRONMENT: AN ATTEMPT TO MODIFY DIRECTIONAL SENSITIVITY IN THE RETINA

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SUMMARY

1. Rabbits were raised inside drums with vertical stripes painted on the inside. The rabbits were held stationary while the drum rotated continually around them: rotation was always in the same direction for any one animal. Rabbits in one litter were put in the drum for 15 min/day from 10–15 days after birth to about 60 days after birth, with the drum rotating to the right. Rabbits in another litter were put in for 15 min/day with the drum moving left. Rabbits in three other litters were put in for 2–3 hr/day with the drum moving right. All rabbits were kept in the dark when not in the drum.

2. Optokinetic nystagmus was measured by photographing eye movements during drum rotation at various stages of development. The response to rotation in both directions was measured in a few adult animals. Only small differences were found in the adult animals between optokinetic nystagmus in response to a drum moving right compared to a drum moving left.

3. Recordings were made from ganglion cells in the retina and their receptive fields were mapped. A total of 607 cells from deprived rabbits were analysed. The percentages of on-centre and off-centre centre-surround types, on-off directionally sensitive types, and on-directionally sensitive types were not significantly different from normal.

4. The percentages of directionally sensitive cells responding in the anterior, posterior, superior and inferior directions were normal. The fall-off in sensitivity for these cells with change in direction from the preferred direction was normal.

5. A few orientation sensitive cells were found responding to horizontally oriented bars.

6. We conclude that this selective deprivation of rabbits had little effect on the optokinetic response and no effect on the organization of the retina.

INTRODUCTION

Kittens which are visually deprived during development grow up with substantial and permanent deficits in their visual system. The first demonstration of the physiological mechanisms involved in one of these deficits was in kittens raised with one eye occluded by suturing the eyelids shut for 2–3 months from birth (Wiesel & Hubel, 1963). At the end of this period, cells in the visual cortex of these kittens are driven almost entirely by the normal eye. The eye which has been shut is functionally disconnected from the cortex, and it is not surprising that acuity is reduced for vision in this eye, or that several tasks depending on vision cannot be performed adequately (Riesen, Kurke & Mellinger, 1953; Ganz, Fitch & Satterberg, 1968; Dews & Wiesel, 1970). The extent of the deficit depends on the age at which the eyelids are sutured (Wiesel & Hubel, 1963): 4–6 weeks after birth is the age at which the cortex is most affected by this kind of deprivation (Hubel & Wiesel, 1970).

The most distinct effects are seen when visual deprivation is selective. Suturing one eyelid shut is selective in the sense that only one eye is closed: when both eyes are closed, the majority of the cells in the visual cortex retain their connexions with both eyes (Hubel & Wiesel, 1965). Other types of selective deprivation lead to other changes in cortical cells. After raising kittens in an environment of vertical stripes, most cortical cells respond to vertically oriented objects, while almost none respond to horizontally oriented objects (Hirsch & Spinelli, 1970, 1971; Blakemore & Cooper, 1970). Humans who are probably born with gross astigmatism have poor acuity as adults along one axis compared to the other, even when the astigmatism is optically corrected for testing (Freeman, Mitchell & Millodot, 1972). Other more subtle changes in the visual environment, for example strabismus, vertical disparity or discontinuous illumination, can also lead to changes in the organization of the visual cortex (Hubel & Wiesel, 1965; Shlaer, 1971; Hirsch, 1972; Cynader, Berman & Hein, 1973). The mechanism involved in these changes of organization is believed to be competition between synaptic terminals of input cells for space on the body and dendrites of an output cell, with the processes of stimulated input cells taking over space from the processes of unstimulated ones. The evidence for this, so far only suggestive, comes from a comparison of the sizes of cells in the layers of the lateral geniculate after various histories of monocular and binocular deprivation (Guillery & Stelzner, 1970; Guillery, 1972).

These effects all involve the cortex and geniculate rather than the retina. Experiments on the retina after lid suture show quantitative rather than qualitative effects, such as changes in the thickness and number of synapses in the inner plexiform layer (Weiskrantz, 1958; Sosula & Glow, 1971; Fifkova, 1972*a*, *b*) and reduction in the amplitude of the b-wave of the e.r.g. in the cat (Hubel & Wiesel, 1963; Hamasaki & Pollack, 1972), although the latter is apparently not true in the rabbit (Reuter, Legein, Van der Mark & Van Hof, 1971). Recordings in the lateral geniculate of cats raised with eyelids sutured shut show that the percentage of Y cells (which respond primarily to movement) is reduced compared to the percentage of X cells (which respond primarily to contrast) (Sherman, Hoffman & Stone, 1972). This is probably the result of geniculate reorganization rather than retinal reorganization (Sherman & Stone, 1973).

One can argue that the failure to find much effect of deprivation on the retina is due to the retina being less plastic than the cortex. Alternatively one can argue that the types of deprivation tried so far are selective for one class of cortical cells versus another, but not selective for one class of retinal cells versus another. We have attempted to distinguish between these two possibilities, by using an animal with fairly complex retinal receptive fields so that selective deprivation would be possible. We chose the rabbit because its retina contains a high percentage of directionally sensitive cells (Barlow, Hill & Levick, 1964). In addition rabbits breed easily and their retina is believed to be still developing a week or more after birth (Noell, 1958). This paper describes the effects of raising rabbits inside vertically striped drums that were continually rotated in one direction only, on the types of receptive field of retinal ganglion cells.

METHODS

Animals. Pregnant pigmented rabbit does were obtained about 1–2 weeks before term, and were placed in a large cardboard box containing straw and food, in a quiet location, about 3–6 days before term. At 6–10 days after birth, the rabbits were moved into cages in the dark. The mother was removed at 4–5 weeks after birth. The only times that the young rabbits were removed from the darkroom were for sessions in the drum or for electrical recording from the retina. We also recorded from the retinas of a number of normal pigmented rabbits.

Selective visual experience. At age 10–15 days, the rabbits were placed, one at a time, in a holder with a cushioned neck clamp and adjustable sides. The holder was placed on a platform inside a drum which could be rotated at an adjustable speed by a motor from which the drum was suspended. The inside of the drum was covered with vertical black and white stripes of variable width and illuminated from above. When the rabbit was positioned with its head on the axis of drum rotation, the drum extended from 17 to 26° below, to about 66° above the level of the rabbit's eye. The stripe widths at eye level subtended between 1·9 and 18° at the

rabbit's eye. The luminance of the white stripes was about 25 cd/m^2. Some rabbits were placed in the drum for 15 min/day with the drum rotating at 3·75°/sec to the right (Litter 1) or to the left (Litter 2). Others (Litters 4–6) were placed in the drum for 3 hr/day with drum rotation to the right. The drum speed before the onset of optokinetic nystagmus (OKN) was 24°/sec. After the onset of OKN, for faster drum speeds, the rabbits' eyes remained motionless for a fraction of the time (see Results). The drum speed was adjusted so that this fraction was substantial. The maximum drum speed was 180°/sec.

Photography. At various stages of development, OKN was photographed using a Beaulieu R-16 motion picture camera fitted with a zoom lens. Film speeds were 4–16 frames/sec and illumination was provided by a lens-end flashlight bulb close to the eye (CM8-503, 6·3 V, 0·35A, Chicago Miniature Lampworks). These bulbs provide about 100–300 cd in the forward direction, at 6 V. Eye position was measured as pupil displacement on projected film, and converted to angular position using Hughes' schematic eye (1972) scaled according to overall eye dimensions. The importance of high speeds of drum rotation and photography to measure OKN was not realized until after raising Litters 1 and 2. (Litter 3 was used to establish methodology for measuring OKN.)

Preparation for recording. Experiments were performed on animals aged 3–7 months, weighing 1·6–3·4 kg. Animals were anaesthetized with halothane, 2·0–4·0 % (Fluothane, Ayerst). Wound areas were infiltrated with a long-lasting procaine anaesthetic. A tracheal cannula and a femoral vein cannula were inserted, and incisions made through the external ear into the auditory canal for inserting ear bars. The eyelids and some of the cartilage around the orbit were removed, the extraocular muscles were cut and the conjunctiva was sutured to a stainless-steel ring near the limbus. Care was taken to keep the eye in its original position relative to the head.

After heart rate and temperature probes were connected, the animal was positioned on a heating pad with ear bars and a chin bar in place, and a muscle relaxant was administered. Either gallamine triethiodide (Flaxedil, Davis & Geck) was infused (initial dose about 3·2 mg/kg, maintenance dose 3·2 mg/kg hr) or D-tubocurarine chloride was injected I.M. (3 mg/kg every 3 hr). The animal was respired with a small animal respiration pump (Harvard Apparatus Co.) with 50 % N_2O + 50 % O_2: respiration parameters were adjusted to maintain a tracheal CO_2 concentration of 4·0–5·0 %, checked periodically with an infra-red CO_2 analyser (Beckman Instruments, Inc.). Some animals were respired with 66 % N_2O + 32·3 % O_2 + 1·7 % CO_2.

The ring sutured to the eye was connected to a ball and socket assembly, through which the electrode driver system passed. A small incision was made in the eye behind the ciliary region and the outer tube of the driver system was inserted. The electrode was advanced to the retina under visual guidance, using an ophthalmoscope. Most units were recorded from altitudes greater than 10° above the horizontal in the visual field. In this way we avoided recording from the visual streak, where a smaller percentage of units are directionally sensitive (Oyster, 1968). The pupils were dilated with atropine and contact lenses were fitted to make a screen at 0·5 m approximately conjugate with the retina, as determined by streak retinoscopy.

Recording and stimulation. Electrodes were tungsten in glass (Levick, 1972). The input was led off to conventional amplification and display equipment. Various stimulus shapes and sizes were projected on a vertical screen, or shapes cut from black paper were held against a uniformly illuminated screen. On some occasions, post-stimulus time histograms were collected. In these cases, projected stimuli were swept across the receptive field by means of a mirror mounted on a galvanometer pen-motor near the projector. Histograms were collected, displayed and recorded

on magnetic tape with the help of a pulse window (which generated a standard pulse when an action potential satisfied certain adjustable criteria) and a LINC computer on-line.

Determination of preferred directions. When a directionally sensitive unit was isolated, it was first mapped with moving and stationary spots. Next, the directional response was estimated by listening to the response over a loudspeaker while the spot was swept through the receptive field in 8 directions (at 45° intervals around the clock) and assigning values to the response magnitude from 0 to 10. The same process was then repeated using a bar wider than the receptive field, moved perpendicular to its length. If the unit responded to the moving bar over 180° or more, the two opposite directions giving equal responses were plotted; if the unit responded over less than 180°, the directions for a criterion threshold response were plotted. If the maximum response occurred over a fairly narrow range of angles, these directions were also plotted. (On several occasions, the perpendicular to the equal-response directions or the bisector of the threshold directions differed significantly from the preferred direction determined directly). There are three advantages to plotting directions with a long bar: (i) it avoids the difficulty of crossing the exact centre of the receptive field (if such a point exists), (ii) the direction of movement is less subject to error, since the bar, in effect, can only move perpendicular to its length, and (iii) a significant percentage of directionally sensitive units are more precisely tuned for direction for a long bar than for a spot (see Results).

Co-ordinates for directions. For each unit, the position and preferred direction were determined relative to the position of the animal's head. During the experiment, the location of the projection of the large blood vessels running transversely from the optic disk was plotted. After an experiment, the positions and preferred directions were computed for the reference frame in which the blood vessels were horizontal. All data for preferred directions are given in this reference frame as if plotted on a screen tangent to the visual sphere at the receptive field. Angles for directions on this screen are measured in the posterior sense from the longitude line passing through the receptive field (0° pointing up) as seen from the rabbit's eye.

RESULTS

Eye movements

It is difficult to ensure that the visual stimulus always moves in the same direction across the retina. The rotation of the drum leads to optokinetic nystagmus, and the lag of the eyes behind the drum may be quite small. This is particularly true in the rabbit, whose visual system fixates on the world quite tightly, whether the world is stationary or mobile (Ter Braak, 1936). It is impractical to stop the eyes from moving by surgery, drugs or mechanical means if the animals are young ones that have to be kept all the time in the dark or in rotating drums. Our solution to the problem was to rotate the drum sufficiently fast that the eyes could not keep up with it all the time.

According to Ter Braak (1936), a rabbit's eyes will follow a drum rotating at 30°/sec quite well. At 50°/sec there is considerable lag; at 72°/sec the eyes make very slow movements, and at 90°/sec, there is almost no eye movement at all. Collewijn (1971) shows somewhat different results,

with the gain (angular eye speed/angular drum speed) falling from nearly 1 at about 3°/sec to 0·5 at 10–30°/sec. It was essential for our experiments that the angular velocity of the stimulus across the retina be not so fast that the directionally sensitive cells would be unstimulated. Fortunately directionally sensitive cells in the rabbit retina respond to a wide range of stimulus velocities, up to 150°/sec or more. Thus a drum speed of 40–60°/sec seemed appropriate.

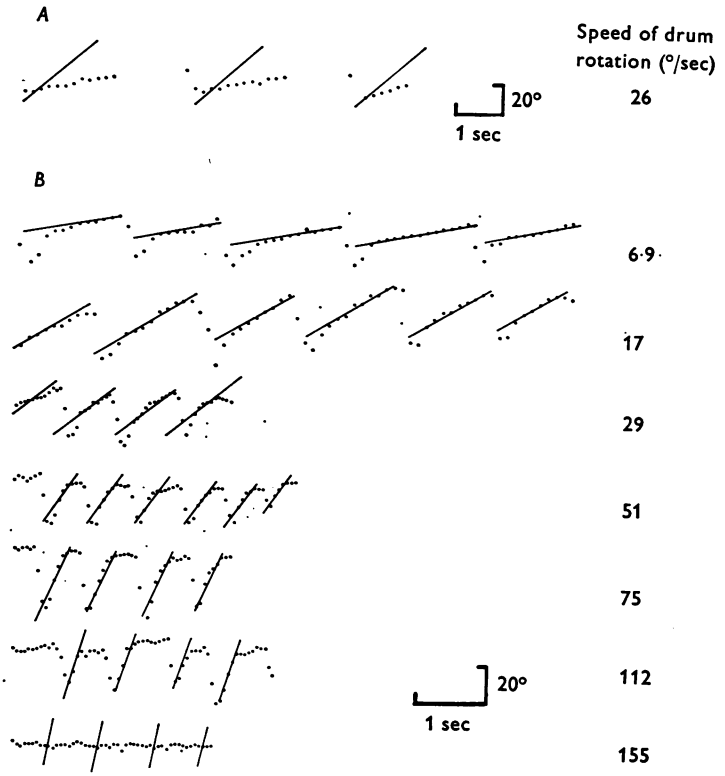

Fig. 1. Eye movements of a rabbit during development. Dots indicate the positions of the eyes; lines show the actual speed of the drum. Lines are placed to fit the dots by eye. *A*, a 12-day old rabbit looking at a drum rotating at 26°/sec. *B*, a 29-day old rabbit looking at a drum rotating at various speeds.

We found that there were two stages in the development of optokinetic nystagmus in the conditions of our experiments. Until 2·5–3 weeks of age the rabbits did not move their eyes very much. At least part of the time the eyes were closed. When the eyes did attempt to follow the drum, the eye movement was slow compared to the drum (Fig. 1*A*). After 2·5–3 weeks from birth, optokinetic nystagmus became distinct. In fact, the eyes

would often follow the drum at much higher speeds (120°/sec) than the results of Ter Braak (1936) and Collewijn (1971) suggest. The tendency at high speeds was for the eyes to follow for a fraction of a second, then remain stationary for a fraction of a second before flicking back (Fig. 1*B*, speeds 51, 75 and 112°/sec). At slow speeds there was often an initial eye movement, during the slow phase of the nystagmus, which went *faster* than the drum (Fig. 1*B*, speeds 6·8, 17 and 29°/sec). This was unexpected, and made us particularly careful to run the drum at a fast enough speed, since whenever the eye moves faster than the drum, the stimulus moves in the wrong direction across the retina.

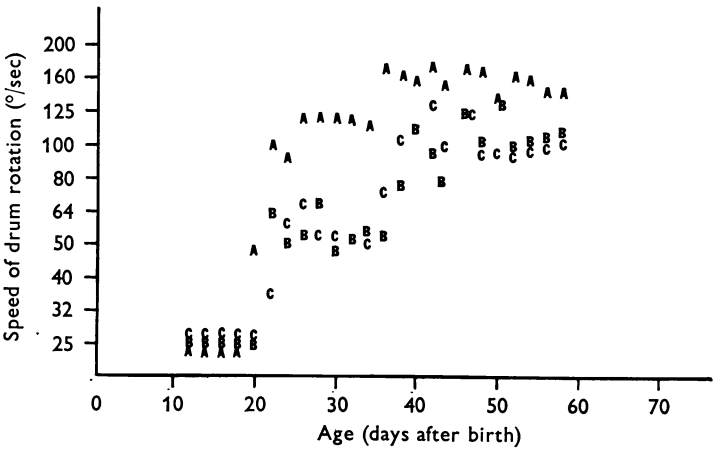

Fig. 2. Speed of rotation of the drum for the three rabbits of Litter 4 at various ages.

A typical regime for the speed of drum rotation is given in Fig. 2. The Figure shows the speeds used for the three rabbits in Litter 4. Until 19 days of age all rabbits were kept in a drum at 24°/sec. After that the speed was increased, up to 180°/sec in some cases. Rabbit *A* developed stronger optokinetic nystagmus than the others, and was therefore put in a drum moving at a faster speed. Eye movements of all animals were observed through a telescope to ensure that the eyes remained stationary a substantial fraction of the time.

We wished to see if there were any behavioural effects of the selective deprivation such as an asymmetry of eye movements. At the end of the period of selective deprivation, a limited number of rabbits were placed in a drum which was rotated first in one direction then in the other. We did not wish to expose most of the rabbits to this in case it might negate the earlier unidirectional experience, although the exposure to the wrong direction of rotation was less than 5 min at each speed and the rabbits

were two months old or more. The results are shown in Fig. 3. At first glance the eye movements appear to follow the drum well for both directions of rotation, and there appears to be little difference between the response to movement left and movement right. However there are slight signs of the eye moving faster than the drum for rightward movement (speeds 4·3 and 13°/sec right), as in Fig. 1*B*, but not for leftward movement. It is as though the prolonged exposure to rightward movement at a fast speed leads to a long-lasting tendency to flick the eyes fast to the right, even when a slowly moving stimulus is presented.

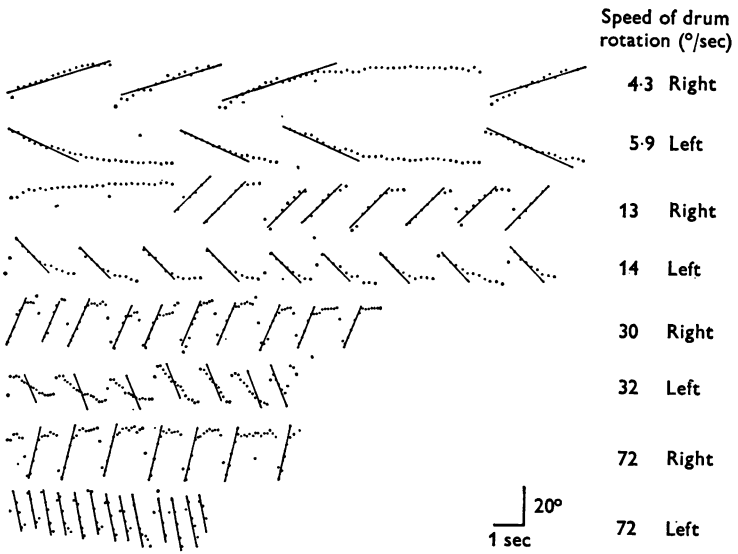

Fig. 3. Eye movements of a 75-day old rabbit, after raising in a drum moving right to the age of 68 days. Dots represent eye positions, lines the speed of drum rotation as in Fig. 1.

Receptive field characteristics

We observed several properties of directionally sensitive units while recording from normal and selectively experienced rabbits that are pertinent to the experiments described here.

Directionality for large vs. *small stimuli.* Most directional units are more specific for the direction of a moving stimulus when the stimulus is large than when it is small (i.e. more specific for a long bar or edge moved perpendicular to its length than for a small spot or a narrow tongue moved along its length). Fig. 4 shows a clear-cut example of this property in a unit. The unit was tested with the stimuli shown in the inset; a long bar moved along its length, and a large rectangle of the same length.

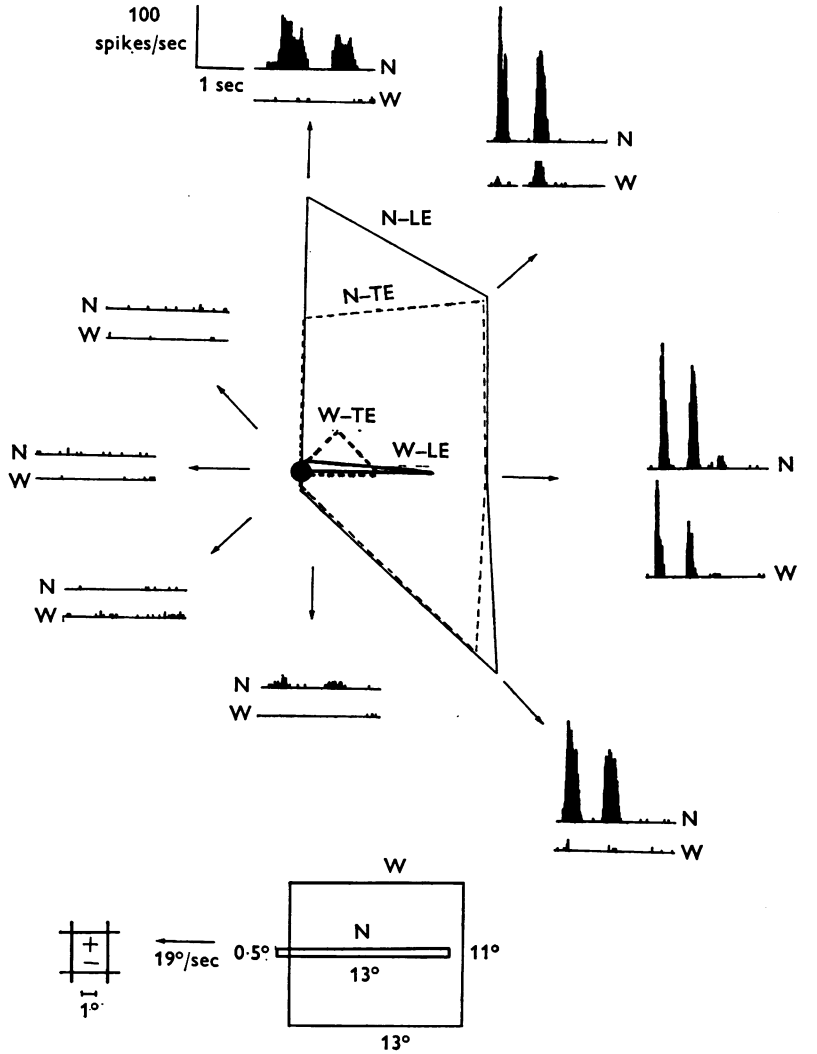

Fig. 4. Responses of an on-off directionally sensitive cell to a narrow bar and a wide bar moved through its receptive field in various directions. Speed of stimuli 19°/sec. Size of stimuli shown at bottom of Figure, in relation to the size of the receptive field. Responses are shown around the edge in the form of a computer plotted histogram, bin width 16·6 msec, 10 responses/histogram. Continuous and dashed lines in the centre represent the amplitude of the responses, by distance from the centre at the Figure. Dashed lines represent trailing edge responses (TE), continuous lines leading edge responses (LE), thin lines responses to a narrow stimulus (N), thick lines responses to a wide stimulus (W).

Response histograms are shown for each of the eight stimulus directions: the upper histogram for each pair is the response to the narrow stimulus, and the lower is the response to the wide stimulus moved in the same direction at the same speed. In a single histogram, the first peak is the response to the leading edge of the stimulus and the second peak is the response to the trailing edge. The frequencies of firing indicated for the histogram are only meaningful when a significant number of spikes occur in any bin. The polar co-ordinate graph in the centre of the Figure shows the number of spikes in each response. The range of directions over which the unit responds is considerably smaller for the wider stimulus. Similar properties have been described for directionally sensitive units in the pigeon (Miles, 1972; A. L. Pearlman & Hughes, C. P., personal communication).

This property can be observed by looking at the responses to movement perpendicular to the preferred direction. About 1 % or fewer directionally sensitive units showed no response to a small spot moved perpendicular to the preferred-null axis, while about 40 % showed no response to a wide bar moved in this manner.

The unit of Fig. 4 is one end of a continuum. Most units showed a smaller increase of directional specificity for a wide stimulus. Fig. 5 depicts a unit whose responses to a spot and a bar were similar. The arrangement of the Figure is similar to Fig. 4, except that a dashed circle is inserted to show the level of spontaneous activity (the unit of Fig. 4 had a very small spontaneous firing rate). The responses to a spot and a bar in most directions are similar, the response to a bar being generally smaller, and in some directions showing more inhibition.

Optimum design of selective experience. The receptive-field properties described above indicate that the best stimuli are moving stripes, as they will isolate a subset of directionally sensitive units as well as possible. Stripes also have the advantage that a movement of the animal's head or eyes perpendicular to the direction of stripe movement produces no retinal stimulation in an up or down direction. (These arguments apply fully only insofar as directionally sensitive units in infant rabbits have the properties found in adults, and this has not been investigated.)

The fact that many on-off directionally sensitive units respond to stimulus movement perpendicular to their preferred directions dissuaded us from raising unrestrained rabbits in stationary striped drums. A rabbit moving its head from side to side in a vertically striped drum would excite some of the on-off directionally sensitive units from each of the four preferred direction groups. Thus, failure of selective experience to modify the distribution of preferred directions would not allow as strong a statement as a moving stripe experiment.

Response to a movement in the null direction. Most units with non-zero

rates of spontaneous firing showed some inhibition for stimulus motion in the null direction (Barlow *et al.* 1964). The unit of Fig. 5 was inhibited by both narrow and wide stimuli, but the inhibition was more pronounced for wide stimuli, as was generally the case in other units. The

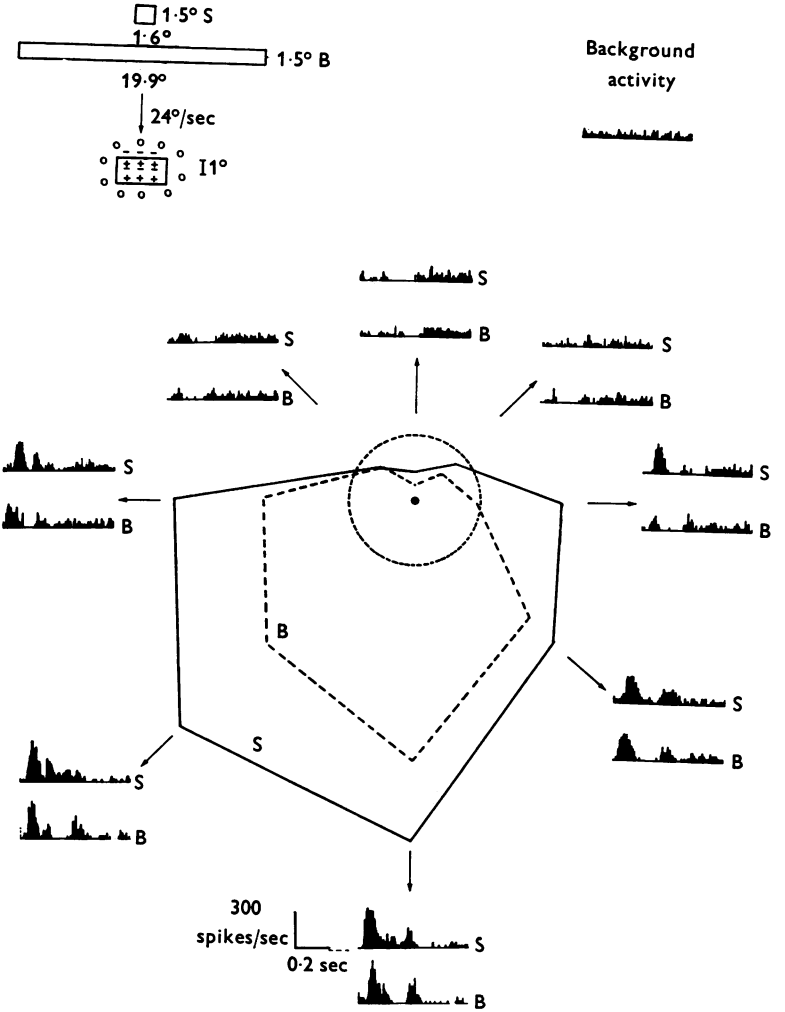

Fig. 5. Responses of an on-off directionally sensitive cell to a spot and a bar moved across its receptive field in various directions. Speed 24°/sec. Inset at top left shows the size of the stimuli in relation to the receptive field. Inset at top right shows the background activity of the cell, when stimulated by a uniform background light. Responses, in the form of a computer plotted histogram, bin width 4·2 msec, 10 responses/sweep are shown around the edge (spot-S, bar-B). Dashed circle shows the level of background activity. Dashed octagon shows the amplitude of the responses to a bar, and continuous line octagon the amplitude of responses to a spot.

greater inhibition for a wide stimulus involves stimulation of the receptive field surround (Barlow & Levick, 1965) as does the common absence of response to wide stimuli moved perpendicular to the preferred direction.

Retinal units in deprived rabbits

Two litters were raised with fairly short experiences per day in the rotating drum. Litter 1 (six rabbits) saw stripes moving to the right and Litter 2 (three rabbits) saw stripes moving to the left, both at 3·75°/sec. Three more litters (nine rabbits) were raised with longer experiences per day, with the stripes moving to the right at speeds exceeding the speed of the slow phase of OKN, as described in the first section of Results. The average amounts of experience per day are shown in Fig. 6. The eyes opened at 10–12 days after birth, and the experience was begun at 10–15 days.

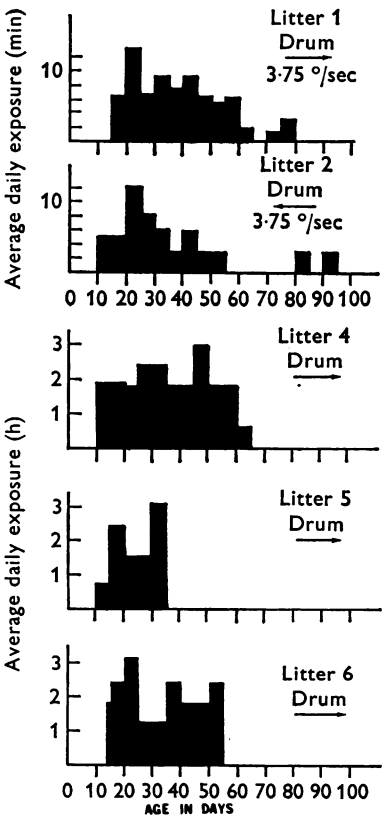

Fig. 6. Exposure of rabbits to the rotating striped drum. Average daily exposure is plotted on the vertical axis against age in days from birth for Litters 1, 2, 4, 5 and 6.

Units were recorded in left and right eyes of rabbits in Litters 1 and 2, and from the right eyes of rabbits in Litters 4–6. In the normal rabbit, there are four groups of on-off directionally sensitive units, with preferred directions approximately anterior, superior, posterior and inferior (Oyster, 1968). The anterior-pointing group is approximately twice as numerous as each of the other groups. Stripes moving to the right would therefore move in the null direction for the anterior-pointing group in the right eye, and it seemed reasonable to expect the greatest effect to occur under these conditions (i.e. the conditions for Litters 4–6).

The numbers of units and the percentages belonging to different receptive-field classes from our experiments, and the percentages from peripheral retina in normal rabbits (Oyster, 1968) are shown in Table 1. There were no systematic differences for the different groups of deprived rabbits in our experiments, so the data were pooled for the third column ('combined'). The percentages for two out of three major classes (concentric on-centre and on-off directionally sensitive) are remarkably similar to the percentages in normal rabbits, and the differences elsewhere can probably be attributed to differences in technique. We did not take particular care to differentiate 'large-field' units (Barlow *et al.* 1964) from off-centre units. Oyster (1968) found 6·2% of the units in peripheral retina to be large-field units, which could account for most of the margin (9·5%) by which our percentage of off-centre units exceeded the percentage found by Oyster. We have no explanation for the low percentage of on directionally sensitive units we found (0·8% for our deprived and 1·6% for our normal rabbits, compared to 4·9%, Oyster, 1968), except that these units are more difficult to detect than on-off directionally sensitive units because they usually respond to much slower stimulus speeds. We have grouped together under 'other and unclassified', units whose receptive fields could not be located, units that were well-isolated but were lost before classification was certain, and units that could not be readily assigned to a particular class. We have also tentatively added two types of unit to the classes already described, namely 'cat-complex' units, which have characteristics like the complex units observed in cat cortex by Hubel & Wiesel (1962), and movement-sensitive units, which respond to stimulus movement but not stationary flashed spots of light and are not directionally sensitive.

Directionally sensitive units in Litters 1 and 2. Fig. 7 shows the preferred directions for the directionally sensitive units recorded. The directions are plotted with anterior towards the centre of the Figure, as seen by the left and right eyes of the rabbits. Comparison of the left side of the Figure with the right shows that there was no obvious difference between the preferred directions in a single litter, regardless of whether the left or right

TABLE 1. Percentages of receptive field types

Receptive field type	Litters 1 and 2	Litters 4–6	Combined	Normal	Normal peripheral retina (Oyster, 1968)
Concentric					
on-centre	32 (23·0 %)	121 (25·9 %)	153 (25·2 %)	43 (23·8 %)	23·9 %
off-centre	49 (35·3 %)	228 (48·7 %)	277 (45·6 %)	73 (40·3 %)	36·1 %
Directionally sensitive					
on-off type	44 (31·7 %)	91 (19·5 %)	135 (22·2 %)	47 (26·0 %)	21·1 %
on type	2 (1·4 %)	3 (0·7 %)	5 (0·8 %)	3 (1·6 %)	4·9 %
off type	1 (0·7 %)	—	1 (0·2 %)	—	(1 unit?)
On-off *not* directionally sensitive	4 (2·9 %)	3 (0·7 %)	7 (1·2 %)	5 (2·8 %)	2·4 %‡
Uniformity-detector	—	1 (0·2 %)	1 (0·2 %)	—	1·2 %
Orientation-sensitive					
horizontal	—	2 (0·4 %)	2 (0·3 %)	—	0·7 %
vertical	—	1 (0·2 %)	1 (0·2 %)	—	0·4 %
Cat-complex*	—	2 (0·4 %)	2 (0·3 %)	—	—
Movement-sensitive†	1 (0·7 %)	—	1 (0·2 %)	—	—
Other and uncharacterized	6 (4·3 %)	16 (3·3 %)	22 (3·6 %)	10 (5·5 %)	9·3 %§
Total no. in sample	139 (100 %))	468 (100 %)	607 (100 %)	181 (100 %)	577 (100 %)

* Units responding optimally to a thin bar moved perpendicular to its length in one direction. There is a minimum length but no maximum length, and the maximum effective thickness is much smaller than the receptive field dimensions. One receptive field was all on, as mapped with flashed bars, the other was on-off.

† No response at all to stationary stimuli. Not directionally sensitive.

‡ Local-edge detectors, as described by Levick (1967).

§ Includes 'large-field' units (6·2 %): these were usually classed with off-centre concentric units by us, accounting for the differences between our results and Oyster's, for off-centre units.

eye was studied. (It should be kept in mind that, for a rabbit in Litter 2, for example, the stimulation during rearing was anterior-to-posterior for the left eye and posterior-to-anterior for the right eye.) There may have been some slight difference between the two litters, but, insofar as it existed, it did not seem to be dependent on the stimulation that a given eye experienced during rearing.

On-off directionally sensitive units in Litters 4–6. The preferred directions of units from the right eyes of Litters 4–6 (which received extensive anterior-to-posterior stimulation during rearing) are shown in Fig. 8.

Only on-off units from altitudes below 55° are shown, these altitudes being below the top of the drum. The preferred directions clustered into four groups, as in normal rabbits: the preferred directions of a similar number of units recorded from normal rabbits (Oyster, 1968) are shown in the inset, and it may be seen that the two distributions are strikingly similar, although some differences are evident. Table 2 gives the mean directions, standard deviations and percentages of units in each group for the units of Fig. 8 and for units from normal rabbits. We found the same

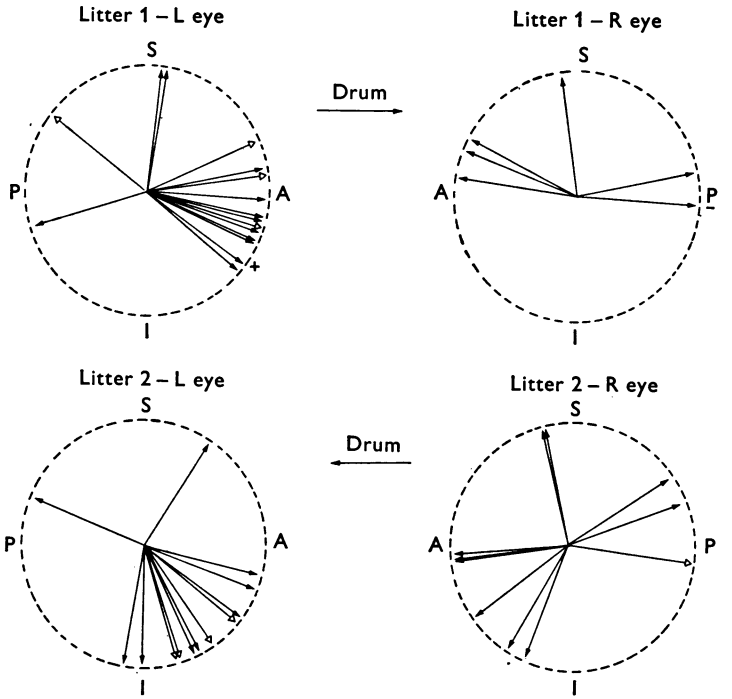

Fig. 7. Preferred directions for the directionally sensitive units in Litters 1 and 2. Units in left eye plotted with anterior direction to right, units in right eye with anterior to left. Filled arrow heads represent units between 0 and 55° up, open arrow heads units above 55° from horizontal. + signifies an on directional unit, − an off directional unit. All others were on-off directional units.

percentages of units with preferred directions anterior and posterior, fewer inferior and more superior than Oyster (1968). The mean preferred directions of our four groups are rotated an average of 12·8° counter-clockwise (as seen by a right eye) with respect to those of Oyster (1968). We do not regard these differences as significant, in the context of this experiment. The percentages of on-off directionally sensitive units which

responded to movement of narrow stimuli or wide stimuli perpendicular to the preferred direction were about the same in deprived rabbits as in the normal rabbits we have studied.

It might be suggested that the rabbits in these experiments saw stripes

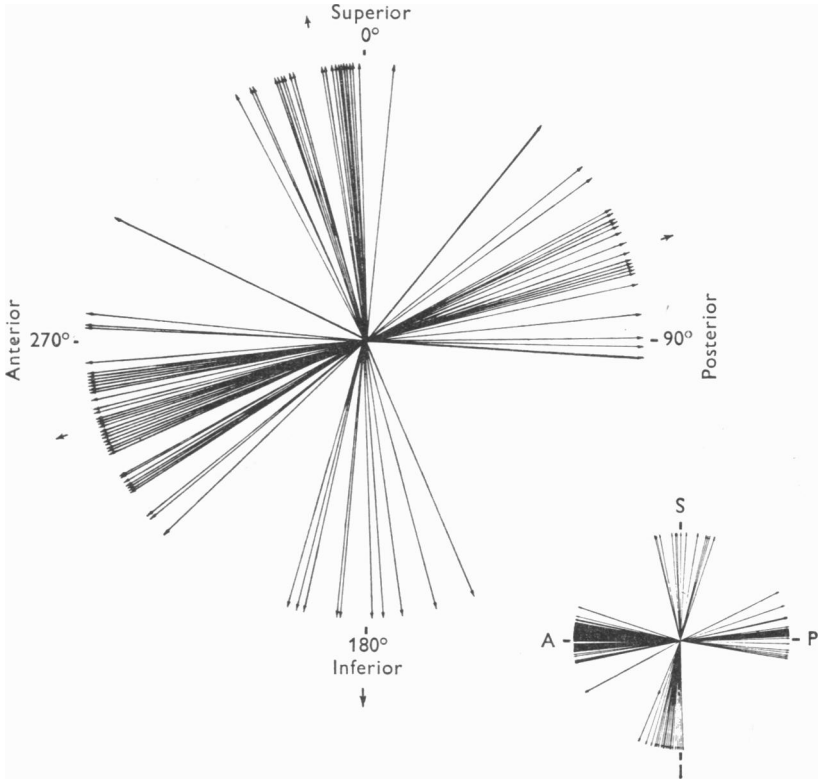

Fig. 8. Preferred directions for the directionally sensitive units in Litters 4, 5 and 6. Arrows at edge of Figure show the average direction for each group. Inset shows the comparable data from Oyster (1968).

TABLE 2. On-off directionally selective units. Comparison of 'highly experienced' rabbits (Litters 4–6) with normals

	Normal (Oyster, 1968)			Selectively deprived		
Group	Average preferred direction (°)	S.D. (°)	(%)	Average preferred direction (°)	S.D. (°)	(%)
Anterior	271·8	± 8·4	44·2	252·7	± 14·1	41·6
Superior	358·2	± 11·5	13·7	350·2	± 8·6	23·6
Posterior	86·6	± 8·9	22·1	70·8	± 12·9	23·6
Inferior	188·5	± 6·5	20·0	180·4	± 12·2	11·2

which were rotated counter-clockwise with respect to the superior and inferior group axes for normal rabbits, and this somehow 'reset' the axes for preferred direction orientation in all four groups of units. However, when rabbits were examined in the holding apparatus, the blood vessels corresponding to the horizontal axes in Fig. 8 were either horizontal or lower at the anterior end, which would be expected to give the opposite shift to that observed. This supports the idea that the differences between our results and Oyster's, for on-off directionally sensitive units, are not a result of early experience.

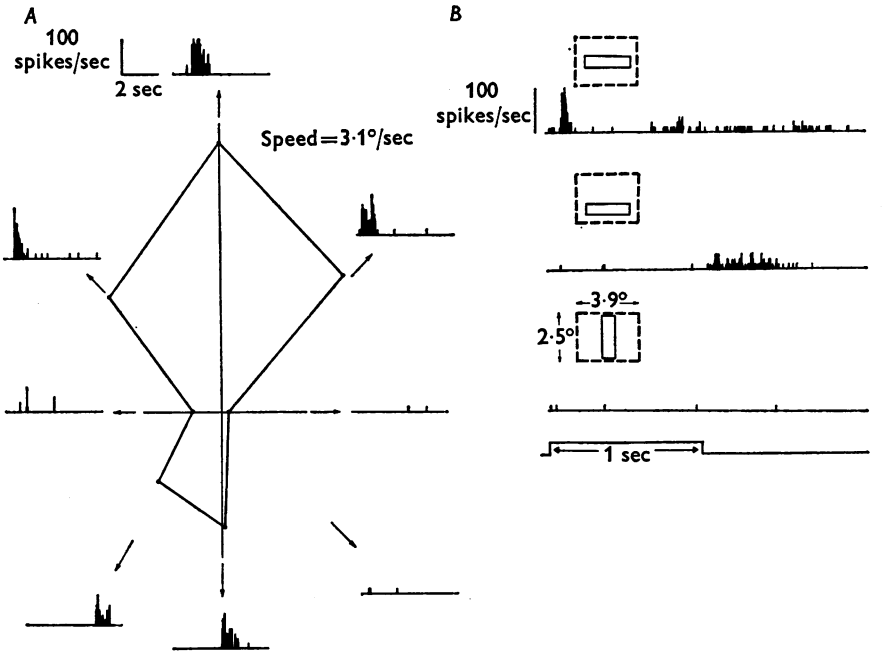

Fig. 9. Orientation sensitive unit from deprived rabbit retina. *A*, responses to a bar moved through the receptive fields in various directions at 3·1°/sec. Responses given as computer plotted histograms, bin width 33 msec, two responses in each histogram. Octagon represents the amplitude of the responses. *B*, responses to a stationary bar flashed in various orientations and various positions in the receptive field. Twenty responses in each histogram, bin width 4·2 msec.

The dispersion of preferred directions in the four groups in our experiments is about one third greater, on average, than in Oyster's data (1968). Oyster found greater dispersion in units above 40° latitude in the visual field, and our data include units from the 40–55° region; however, discarding these units from our data did not produce a significant reduction in dispersion. The five units observed at latitudes above 55° were poorly

aligned with the average directions in the groups to which they belonged, but the differences were not systematic.

Other units sensitive to stimulus direction or orientation. In recording from units in rabbits in Litters 4–6, we found three types of units, besides the on-off directionally sensitive type, which were sensitive to stimulus direction and/or orientation: on-type directionally sensitive, orientation-sensitive and 'cat-complex' units. The last type of unit was observed twice, once preferring a horizontal stimulus moved superior-to-inferior, and once preferring a vertical stimulus moved anterior-to-posterior. Of the three on type directionally sensitive units observed, two preferred motion inferior-to-superior and one preferred motion approximately anterior-to-posterior. Of the three orientation-sensitive units observed, two preferred a horizontal stimulus and one preferred a vertical stimulus. An orientation unit from Litter 6 is shown in Fig. 9: the responses to a bar flashed for 1 sec in various positions are shown on the right, and to the same bar moved perpendicular to its length, on the left. The bar was moved at 3·1°/sec, but the unit responded well at speeds up to 50°/sec or more. Note that the large response to a bar moved inferior-to-superior is consistent with the responses to stationary bars, which show an off-zone located inferior to an on or on-off zone.

Examples of each type of receptive field sensitive to orientation were found with preferred orientations perpendicular to that experienced by the rabbit in early life. No on-type directionally sensitive units with preferred direction anterior (opposite to drum rotation) were observed, but Oyster (1968) found that less than one third of on-type directionally sensitive units have preferred directions anterior, so this finding is not improbable given that only three on-type directionally sensitive units were observed in Litters 4–6.

DISCUSSION

The results of these experiments show that early visual experience does not influence retinal organization. Oyster (1968) showed that the preferred directions for directionally sensitive ganglion cells in the rabbit fall into four groups, anterior, posterior, superior, inferior. If the rabbit retina is plastic, like the cat cortex, and our selective deprivation regime covered the period of plasticity, one would expect one of these groups to disappear. In fact all four groups were found in close to normal percentages. Four possibilities need discussion in relation to these results (i) that occasional movements of a stimulus in the 'wrong' direction across the retina were enough to cancel the effects of the periods that the rabbit spent in the drum, (ii) that movement in the null direction across the receptive field is in some sense a stimulus, as much as movement in the preferred

direction, (iii) that the rabbit visual system is less plastic than the cat visual system, and (iv) that the retina is less plastic than the visual cortex.

There is no doubt that occasional 'wrong way' movements across the retina did occur, in spite of our efforts to rotate the drum at a fast enough speed. However, when Blakemore & Cooper (1970) placed kittens inside vertically striped drums, the kittens occasionally saw horizontal stripes while being put in and out of the apparatus, and when Hirsch & Spinelli (1970) raised kittens with vertically striped goggles on their heads, the goggles occasionally fell off, yet both sets of experiments produced positive results. Moreover, our experiment was a test for orientation deprivation as well as directional deprivation under conditions that were very close to those used by Blakemore & Cooper (1970), as far as stimulation of orientation sensitive cells is concerned. Although the percentage of orientation cells in the rabbit retina is very small, we did find about the normal percentage of such cells, including some specific for horizontal orientations. Our rabbits did not observe horizontal lines any more frequently than Blakemore and Cooper's cats.

The possibility that movement in the null direction across the receptive field is in some sense a stimulus is hard to evaluate. While hypotheses have been put forward concerning the mechanism of directionally sensitive cells in the retina (Barlow & Levick, 1965; Werblin & Dowling, 1969), the mechanism is not known. One can hypothesize that synapses are the plastic elements in the nervous system, and that as long as a synapse is active, it will be maintained, irrespective of whether it is an excitatory synapse or an inhibitory synapse. It is certainly possible that inhibitory synapses from amacrine cells on to ganglion cells are involved in directional sensitivity, and that movement of a stimulus in the null direction is enough of a stimulus to maintain them, and consequently enough to maintain the directional sensitivity of the ganglion cell.

The possibility that the cat's visual system might be more plastic than the rabbit's is related to the possibility that the retina might be less plastic than the cortex, because the types of receptive field found in the rabbit retina are similar to those found in the cat cortex. The rabbit retina contains cells specific for orientation, which would be classed as simple or complex in the Hubel & Wiesel terminology for the cat. In one sense the directionally sensitive cells of the rabbit retina are hypercomplex: the response for a long bar moved perpendicular to the preferred-null axis is less than the response for a short bar. In reality the simple, complex, hypercomplex terminology is inappropriate in the rabbit visual system, because it implies a hierarchy of cell types that has not yet been established for the rabbit. If a hierarchy is established it will certainly be

different from the hierarchy in the cat. This point is underlined by the suggestion that simple cells in the rabbit cortex develop at a later stage than complex, direction sensitive or motion sensitive cells (Grobstein, Chow, Spear & Mathers, 1973).

One study has been done on the effect on the rabbit cortex of raising rabbits inside stationary striped drums (Mize & Murphy, 1973). The results were negative, like the results in our experiments: in rabbits raised inside vertically striped drums, the percentage of cells responding to horizontal stripes was normal, as was the percentage responding to vertical stripes. Since the drums were stationary, and many directionally sensitive cells respond over an arc of more than 180° (at least in the retina; comparable data for cortical cells are not yet available) no effect on the percentage of various types of directionally sensitive cells would have been expected, and no effect was found. The results as far as orientation sensitive cells are concerned are hard to interpret, because nobody knows whether orientation sensitive cells in the rabbit cortex are simply projections of the orientation sensitive cells in the rabbit retina, or involve connexions and convergence within the rabbit cortex from other types of cell.

The last possibility mentioned above is that the retina is less plastic than the cortex. This is reasonable, because the nervous connexions within the retina are believed to be made at an earlier stage than connexions within the cortex. Anatomically the rabbit retina appears to mature at about the time that the eyes open (Noell, 1958), and recordings from the rabbit superior colliculus also suggest that the rabbit retina must be fairly mature at this time (Spear, Chow, Masland & Murphy, 1972). If there is to be an effect of deprivation, then one has to argue that it is possible for such an effect to occur after the connexions are initially formed, as occurs in the cat cortex. Some direction and orientation sensitive cells have been found in the cat cortex between 2 and 4 weeks by both groups working on this subject, although there is some controversy about the percentages involved (Hubel & Wiesel, 1963; Pettigrew, 1972). This is before the age of greatest susceptibility to the effects of visual deprivation, which is around 4–6 weeks of age (Hubel & Wiesel, 1970). Quite possibly retinal connexions are immutable after they are initially formed, but cortical connexions are not.

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